

Feeding ecology and niche overlap of Lake Ontario offshore forage fish assessed with stable isotopes

James A. Mumby, Timothy B. Johnson, Thomas J. Stewart, Edmund A. Halfyard, Brian C. Weidel, Maureen G. Walsh, Jana R. Lantry, and Aaron T. Fisk

Abstract: The forage fish communities of the Laurentian Great Lakes continue to experience changes that have altered ecosystem structure, yet little is known about how they partition resources. Seasonal, spatial, and body size variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ was used to assess isotopic niche overlap and resource and habitat partitioning among the five common offshore Lake Ontario forage fish species ($n = 2037$; alewife (*Alosa pseudoharengus*), rainbow smelt (*Osmerus mordax*), round goby (*Neogobius melanostomus*), and deepwater (*Myoxocephalus thompsonii*) and slimy (*Cottus cognatus*) sculpins). Round goby had the largest isotopic niche ($6.1\% \pm 2$, standard ellipse area), followed by alewife ($3.4\% \pm 2$), while rainbow smelt, slimy sculpin, and deepwater sculpin had the smallest and similar niche size ($1.7\% \pm 2$ – $1.8\% \pm 2$), with only the sculpin species showing significant isotopic niche overlap ($>63\%$). Stable isotopes in alewife, round goby, and rainbow smelt varied with location, season, and size, but did not vary in the sculpin species. Lake Ontario forage fish species have partitioned food and habitat resources, and non-native alewife and round goby have the largest isotopic niche, suggestive of a broader ecological niche, and may contribute to their current high abundance.

Résumé : Si les communautés de poissons-fourrage des Grands Lacs laurentiens continuent de subir des changements qui ont modifié la structure des écosystèmes, les connaissances sur le partage des ressources dans ces communautés sont limitées. Les variations saisonnières, spatiales et associées à la taille du corps du $\delta^{13}\text{C}$ et du $\delta^{15}\text{N}$ ont été utilisées pour évaluer le chevauchement des niches isotopiques et le partage des ressources et des habitats entre cinq espèces de poissons-fourrage pélagiques répandues du lac Ontario ($n = 2037$; le gaspéreau (*Alosa pseudoharengus*), l'éperlan arc-en-ciel (*Osmerus mordax*), le gobie à taches noires (*Neogobius melanostomus*), le chabot de profondeur (*Myoxocephalus thompsonii*) et le chabot visqueux (*Cottus cognatus*)). Le gobie à taches noires présente la plus grande niche isotopique ($6,1\% \pm 2$, aire de l'ellipse standard), suivi du gaspéreau ($3,4\% \pm 2$), alors que l'éperlan arc-en-ciel, le chabot visqueux et le chabot de profondeur ont les plus petites niches, de tailles semblables ($1,7\text{--}1,8\% \pm 2$), seuls les chabots présentant un chevauchement significatif de leurs niches isotopiques ($>63\%$). Les isotopes stables des gaspareaux, gobies à taches noires et éperlans arc-en-ciel varient selon le lieu, la saison et la taille, contrairement à ceux des chabots. Les espèces de poissons-fourrage du lac Ontario présentent un partage des ressources alimentaires et des habitats, le gaspéreau et le gobie à taches noires, des espèces non indigènes, étant caractérisés par les plus grandes niches isotopiques, ce qui indiquerait une niche écologique plus large et pourrait contribuer à expliquer leur forte abondance actuelle. [Traduit par la Rédaction]

Introduction

In the Laurentian Great Lakes (hereinafter Great Lakes), consumption by the offshore prey fish community transfers production from the lower trophic level to higher trophic levels and can influence abundances and species composition at multiple trophic levels (Mills et al. 2005; Stewart and Sprules 2011; Bunnell et al. 2014). As the Great Lakes food webs change in response to human influences, interactions among coexisting prey fish sharing common food resources and habitat can influence food web structure, change pathways of energy transfer, and impede or enhance the attainment of management objectives. Resource and habitat partitioning promotes the coexistence of sympatric species by reducing competition (Schoener 1974; Ross 1986). Insight into how prey fish species can coexist or potentially compete can lead to a better understanding of the potential food web responses to changing fish community composition.

The Lake Ontario offshore pelagic prey fish community is dominated by non-native alewife (*Alosa pseudoharengus*; Owens et al.

2003). Less abundant offshore prey fish species include the non-native pelagic rainbow smelt (*Osmerus mordax*) and native benthic deepwater (*Myoxocephalus thompsonii*) and slimy (*Cottus cognatus*) sculpins. Invasive round goby (*Neogobius melanostomus*), first sighted in western Lake Ontario in 1998, have become abundant in benthic habitats in both nearshore and offshore regions of Lake Ontario (Owens et al. 2003; Pennuto et al. 2012). Historically, the original offshore pelagic prey fish community was dominated by five species of deepwater ciscoes (*Coregonus* spp.), which have been extirpated, and a shallow-water cisco (*Coregonus artedii*) that still persists at very low numbers (Christie 1973; Hoyle 2015). Bloater (*Coregonus hoyi*), another extirpated deepwater cisco, are currently being re-introduced (Stewart and Lake 2015).

Understanding prey fish community interactions is relevant to emerging issues in Great Lakes restoration and fisheries management. Human influences on the Great Lakes ecosystems have resulted in the decline in some native species and increasing dominance and persistence of non-native species (Mills et al. 2005;

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J.A. Mumby, E.A. Halfyard, and A.T. Fisk. Great Lakes Institute for Environmental Research, University of Windsor, Windsor, ON N9B 3P4, Canada.

T.B. Johnson and T.J. Stewart. Glenora Fisheries Station, Ontario Ministry of Natural Resources & Forestry, R.R. #4, Picton, ON K0K 2T0, Canada.

B.C. Weidel and M.G. Walsh. USGS Lake Ontario Biological Station, Oswego, NY 13126, USA.

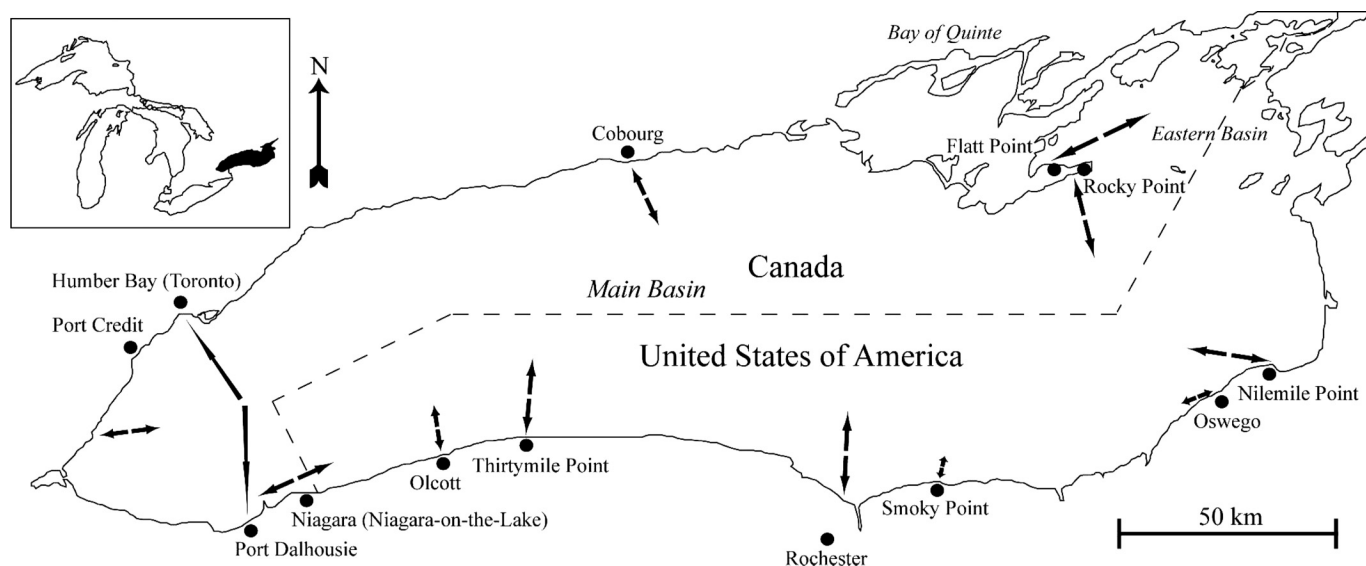
J.R. Lantry. Cape Vincent Fisheries Station, New York State Department of Environmental Conservation, Cape Vincent, NY 13618, USA.

Corresponding author: Aaron T. Fisk (email: afisk@uwindsor.ca).

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Fig. 1. Lake Ontario prey fish sampling sites completed using 12 different transects (six in the USA and six in Canada) in 2013. Transect length and direction are represented by arrow length and position.



Dettmers et al. 2012). In Lake Ontario and other Great Lakes, the alewife are the principal forage fish of non-native salmonid species (O’Gorman and Stewart 1999; Stewart and Sprules 2011) and are required in sufficient abundance to sustain the recreational fishery. However, alewife consume early life stages of native pelagic fish species (Krueger et al. 1995; Madenjian et al. 2008), potentially directly limiting the recruitment of other prey fish and also limiting food resources of other prey fish by consuming most of the available zooplankton production (Stewart and Sprules 2011). Further, a diet high in alewife can impede reproduction of salmonids (Brown et al. 2005). Fisheries management objectives are to sustain the highly valued recreational fisheries and restore self-sustaining populations of native predators and prey fish, including a focus on reestablishing native deepwater cisco (Stewart et al. 1999; Stewart and Lake 2015). A dilemma for fisheries managers is that maintaining high levels of alewife to sustain the recreational fishery may also impede the wild production and restoration of native predator and prey fish species (Dettmers et al. 2012; Stewart et al. 2013). How native and non-native prey species partition food and habitat resources is thus very relevant to this management issue.

Previous research suggests some partitioning of available food and habitat resources among Great Lakes prey fish species (Bunnell et al. 2015); however, no study has examined this in a Great Lake with substantial spatial and season coverage across a suite of prey fishes concurrently. Alewife and rainbow smelt occupy the offshore pelagic habitat with seasonal migration nearshore associated with spawning (O’Gorman et al. 1991). The sculpin species occupy benthic habitat, with the deepwater sculpin distributing further offshore and to greater depths than the slimy sculpin (Madenjian and Bunnell 2008). Round gobies are benthic but occupy both nearshore and offshore habitats, with their depth distribution varying seasonally (Walsh et al. 2007; Pennuto et al. 2012). Young-of-the-year rainbow smelt and alewife spatially segregate during thermal stratification but have high diet overlap (Urban and Brandt 1993). Based on stomach content analysis, diets diverge among the species such that the diets of pelagic species (alewife, rainbow smelt, and ciscoes) are dominated by zooplankton and *Mysis* (*Mysis diluviana*; Walsh et al. 2008; Stewart and Sprules 2011). Sculpins are a major consumer of *Mysis* and, to a lesser extent, benthic invertebrates (Walsh et al. 2008; Hondorp et al. 2011; Stewart and Sprules 2011). Round goby diet is dominated by dreissenid mussels (*Dreissena* spp.) and smaller quantities

of *Mysis*, benthic invertebrates, and zooplankton (Walsh et al. 2007; Taraborelli et al. 2010; Brush et al. 2012), perhaps indicating a unique trophic role for this species. Seasonal or ontogenetic variation in diet and habitat use may increase or decrease the potential for diet and habitat overlap among prey fish species, and alternative approaches to assessing the level of resources and habitat partitioning are warranted.

Stable isotopes of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) are a commonly used and powerful tool to assess trophic relationships, habitat use, and overall food web structure (Cabana and Rasmussen 1994; Post 2002; Fry 2006). Carbon isotopes show limited change with each trophic level step (<1‰) in aquatic food webs but provide quantitative information on carbon sources and habitat use (Hobson and Welch 1992); in lakes, $\delta^{13}\text{C}$ is generally lower in pelagic zones and higher in benthic-littoral zones (France 1995). Values of $\delta^{15}\text{N}$ increase ~3‰–4‰ between prey and consumer (DeNiro and Epstein 1981; Minagawa and Wada 1984; Vander Zanden and Rasmussen 2001) and provide quantitative information on trophic position. Nitrogen isotopes can also vary between habitats (e.g., sediments and above water column; Mulholland et al. 2000) and taken with $\delta^{13}\text{C}$ can provide key information on food web structure and species–population interactions. For example, isotopic niche width can be calculated based on the distribution of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data and can be compared between species or populations in an ecosystem, providing insights on potential competition and niche overlap (Jackson et al. 2011). It is important to stress that isotopic niche, while providing insights on feeding ecology, is not equivalent to quantifying a species ecological niche, and is vulnerable to the same assumptions that traditional isotopic applications have.

The objective of this study was to quantify seasonal, size-related, and regional variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in the five most common Lake Ontario offshore forage fish species (alewife, rainbow smelt, round goby, slimy sculpin, and deepwater sculpin) to assess niche overlap and resource and habitat partitioning among these important species. By utilizing a coordinated Lake Ontario sampling program in 2013, an extremely comprehensive set of samples ($n = 2037$) was collected that gave wide spatial coverage of the lake, seasonal samples (April to November), and range of body sizes. This comprehensive sampling of the forage fish, particularly spatially, allows inferences to be made about the relative trophic relations independently of diet data. The results of this study will provide needed insights on how forage fish partition resources

Table 1. Number of samples by season (spring, summer, fall), bathymetric depth (<30 m, >30 m), and quadrat (NW, NE, SW, SE) per prey fish species collected from Lake Ontario in 2013.

Species	Season			Bathymetric depth		Quadrat			
	Spring	Summer	Fall	<30 m	>30 m	NW	NE	SW	SE
Alewife	327	347	128	223	579	135	328	178	161
Rainbow smelt	177	79	99	85	270	26	128	92	109
Round goby	130	120	198	260	188	50	193	113	92
Deepwater sculpin	111	45	67	0	223	4	25	83	111
Slimy sculpin	85	46	78	0	209	3	54	38	114

and important baseline data for studies on predator fish and food web structure in Lake Ontario.

Materials and methods

Fish collection

Coordinated binational sampling occurred on Lake Ontario in 2013 that involved many Canadian and American provincial-state and federal agencies organized under the Cooperative Science Monitoring Initiative program (Richardson et al. 2012). Prey fishes were collected using a combination of vertical gillnets, horizontal gillnets, seine nets, and trawl nets, set at depths of 1 to 175 m, and fished approximately monthly from April to November 2013. Twelve nearshore-to-offshore transects were sampled to collect prey fish in 2013 (six in Canada and six in the US; Fig. 1). In American waters, the transects completed were Nine Mile Point (depths from 15 to 175 m), Olcott (depths from 15 to 110 m), Oswego (depths from 4 to 50 m), Rochester (depths from 8 to 170 m), Smoky Point (depths from 18 to 78 m), and Thirty Mile Point (depths from 15 to 175 m). In Canadian waters, the transects completed were Cobourg (depths from 1 to 60 m), Flatt Point – Eastern Basin (depths from 5 to 35 m), Rocky Point (depths from 1 to 100 m), Port Credit (depths from 45 to 100 m), Niagara (depths of 18 to 80 m), and a transect across the Western Basin from Port Dalhousie to Humber Bay (from depths of 15 m in Port Dalhousie to approximately 120 m at the maximum to depths of 12 m in Humber Bay).

A variety of techniques were used to collect the prey fish. Seine nets were used to sample waters in near-nearshore (0–5 m depth) locations, and vertical and horizontal gillnets were used to collect samples from the nearshore (5–30 m depth) to offshore pelagic areas (>30 m deep) deployed on the order of hours. Vertical gillnets were used to better sample the water column to 30 m in depth. Benthic areas of the nearshore and offshore (offshore benthic areas, >30 m deep) were sampled using bottom trawls.

During fish collection, fish were identified to species and then stored on ice and processed later in the laboratory. Before dissection, fish were weighed (to nearest 0.1 g), and total length (to nearest 1 mm) was recorded for all species, with only fork length (mm) recorded for alewife and rainbow smelt. Dorsal muscle was removed above the lateral line and posterior to the head, placed in a 2 mL cryovial, frozen, and freeze dried for 48 h at –20 °C for stable isotope analysis. Table 1 provides the distribution of species sample numbers by quadrat, season, and bathymetric depth.

Stable isotope analysis

Approximately 2 g of freeze-dried fish muscle samples were homogenized to a fine powder using either surgical scissors or mortar and pestle, depending on muscle size and density. Bulk (nonlipid extracted) powdered muscle samples were weighed into 5 mm × 9 mm tin capsules on a microbalance with masses between 400 and 600 µg. An elemental analyzer (Costech, Valencia, California, USA) was used to combust the muscle sample into CO₂ and N₂ gases, and the relative abundances of carbon (¹³C/¹²C) and nitrogen (¹⁵N/¹⁴N) were then determined using a Thermo Finnigan Delta V mass spectrometer (Thermo Finnigan, San Jose, Califor-

nia, USA). The carbon to nitrogen ratio (C:N) was measured simultaneously during stable isotope analysis to determine if lipid contents were high in the muscle; C:N ratios <3.4 were considered to have low lipid (Post 2002); mean C:N values for all species were below this 3.4 value.

Standard delta notation (δ) was used to express δ¹⁵N and δ¹³C in parts per thousand (‰) differences from a standard material as follows:

$$\delta^{13}\text{C or } \delta^{15}\text{N} = [(R_{\text{sample}}/R_{\text{standard}} - 1)] \times 1000$$

where $R = {}^{13}\text{C}/{}^{12}\text{C}$ or ${}^{15}\text{N}/{}^{14}\text{N}$ (Fry 1991; Hobson and Clark 1992). Pee Dee Belemnite for carbon and atmospheric nitrogen were used as standard reference materials. During the analysis, National Institute of Standards and Technology (NIST) standards were used to calculate the precision and accuracy of analysis. NIST standards used for δ¹⁵N were NIST 8573 (L-glutamic acid), 8548, and 8547 (both ammonium sulfate) and for δ¹³C were NIST 8573 and 8542 (sucrose) ($n = 96$ for each) and had a difference of ≤0.1‰ for δ¹⁵N and ≤0.1‰ for δ¹³C from the certified values. The analytical precision based on NIST 1577c (bovine liver) and the internal lab standard *Tilapia* ($n = 318$) had a standard deviation of <0.2‰ for δ¹⁵N and <0.1‰ for δ¹³C.

Statistical analysis

Generalized linear models (GLMs) were used to investigate the impact of four explanatory variables on the values of δ¹⁵N and δ¹³C in Lake Ontario prey fish, including (i) total length, (ii) quadrat (a factor centered on differences in lake physiochemical properties; northwest — upwelling, northeast — islands and embayments, southwest — Niagara plume, and southeast — downwelling and abyssal, (iii) season (defined by calendar seasons: spring — 22 March – 21 June; summer — 22 June – 21 September; and fall — 22 September – 21 December), and (iv) bathymetric depth (nearshore (<30 m) and offshore (>30 m)). Nearshore and offshore waters were defined as where the thermocline intersected with the lake bed, which is approximately 30 m in late summer or early fall in Lake Ontario (Edsall and Charlton 1997). This delineation was used also in the spring season. The GLMs used a Gaussian or Gamma error distribution with log, identity, or inverse link function as warranted by the data. A small number of extreme outliers exhibiting high leverage (i.e., high influence on the model) were removed from the analysis. To identify the “best model”, we relied on a sequential deletion approach using likelihood ratio tests (e.g., Crawley 2005), which involved fitting a “maximal” model for each isotope-species combination that included all explanatory variables. After a series of deletion tests (χ^2 or F tests), a minimal adequate model was determined when all remaining terms were significant. The goodness-of-fit of the minimal adequate model was assessed using an approximate likelihood ratio test.

Stable Isotope Bayesian Ellipses in R (SIBER) in the package SIAR version 4.2 (Parnell and Jackson 2013) in R version 3.0.2 (R Core Team 2013) was used to analyze isotopic niche space of the prey fish species in Lake Ontario. Developed by Jackson et al.

Table 2. Length range (mm), total length (mm; mean \pm 1 SE), stable isotopes ratios, and C/N ratio (mean \pm 1 SE) of alewife, rainbow smelt, round goby, deepwater sculpin, and slimy sculpin collected from April to November 2013 across Lake Ontario.

Species	n	Length range	Total length	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	C/N ratio
Alewife	802	10–205	140 \pm 1.4	–24.1 \pm 0.04	12.6 \pm 0.04	4.0 \pm 0.03
Rainbow smelt	355	51–180	110 \pm 1.5	–23.6 \pm 0.02	15.0 \pm 0.07	3.5 \pm 0.01
Round goby	448	9–190	90 \pm 1.5	–21.8 \pm 0.09	13.6 \pm 0.06	3.4 \pm 0.01
Deepwater sculpin	223	59–186	126 \pm 1.7	–24.7 \pm 0.06	16.9 \pm 0.04	4.1 \pm 0.06
Slimy sculpin	209	11–145	97 \pm 1.3	–24.6 \pm 0.05	16.6 \pm 0.05	3.8 \pm 0.04

Table 3. Isotopic niche width (standard ellipse area, SEA_C ; ‰²) for all samples by season, bathymetric depth, and quadrat and overlap (% for all samples) of main prey fish species collected from Lake Ontario in 2013.

Species	SEA_C (‰ ²)	Season (‰ ²)			Bathymetric depth (‰ ²)		Quadrat (‰ ²)				Isotopic overlap (%)				
		SPR	SUM	FAL	<30 m	>30 m	NW	NE	SW	SE	ALE	RBS	RDG	DWS	SLS
ALE	3.4	2.3	2.5	3.1	3.4	3.3	4.3	2.6	3.6	3.7	—	0	0	0	0
RBS	1.8	1.8	1.4	0.9	2.1	1.7	1.5	1.6	1.2	2.3	0	—	4	0	0
RDG	6.1	7.6	5.5	4.8	5.5	4.0	3.2	4.4	4.1	5.6	0	15	—	0	0
DWS	1.8	1.6	2.6	1.6	NA	1.8	—	1.2	1.3	1.3	0	0	0	—	69
SLS	1.7	2.0	1.2	1.3	NA	1.7	—	2.3	1.5	1.1	0	0	0	63	—

Note: No samples were collected <30 m for either sculpin species, and <10 sculpin species samples total were collected in the northwest (NW) quadrat. For isotopic overlap, read in the left to right direction (i.e., rainbow smelt SEA_C overlaps only 4% of round goby SEA_C). Data include SEA_C (‰²) calculated for season (SPR = spring, SUM = summer, FAL = fall), bathymetric depth (<30 m, >30 m), and quadrat (NW, NE, SW, SE) per prey fish species. ALE = alewife, RBS = rainbow smelt, RDG = round goby, DWS = deepwater sculpin, SLS = slimy sculpin.

(2011), SIBER uses a multivariate ellipse-based approach to compare groups of differing sample sizes. Standard ellipse areas (SEA_C) represented the core (40%) isotopic niche area, a common method with SIBER that avoids including individuals at the extremes of the stable isotope data, allowed for a strong comparison for varying sample sizes between species. The SEA_C was estimated using a Bayesian approach (1 000 000 iterations) with increasing SEA_C (‰²) resulting in larger niche areas (i.e., feed across many habitat types and (or) feed across many trophic positions). Calculated using SEA_C , fraction overlap (%) of the prey fish species on prey fish species isotopic niche was used to determine differences and similarities in niche space utilization.

Results

Fish size

Alewife size did not vary by quadrat ($p = 0.57$; ANOVA) or bathymetric depth ($p = 0.50$), but varied with season ($p < 0.01$; spring = 132.8 ± 2.3 mm (mean \pm SE); summer = 146.0 ± 2.0 mm; fall = 141.7 ± 3.6 mm). Rainbow smelt size (mm) did not vary by quadrat ($p = 0.16$) or season ($p = 0.10$) but increased with bathymetric depth of collection ($p < 0.01$; <30 m = 99.9 ± 3.5 mm; >30 m = 113.7 ± 1.6 mm). Round goby size (mm) varied by quadrat ($p = 0.01$; largest in the southeast: 98.0 ± 4.1 mm; smallest in the northeast: 85.7 ± 2.3 mm) but did not vary by season ($p = 0.92$) or bathymetric depth ($p = 0.14$). Deepwater sculpin size (mm) varied by quadrat ($p < 0.01$; largest in the northwest: 137.5 ± 2.9 mm; smallest in the northeast: 95.7 ± 3.1 mm) and increased by season ($p < 0.01$; spring = 121.1 ± 2.1 mm; summer = 123.1 ± 4.5 mm; fall = 136.8 ± 2.9 mm). Slimy sculpin size (mm) varied by quadrat ($p < 0.01$; largest in the northwest: 132.0 ± 1.2 mm; smallest in the northeast: 86.2 ± 2.7 mm) and varied with season ($p < 0.01$; spring = 91.6 ± 2.3 mm; summer = 105.4 ± 2.8 mm; fall = 99.2 ± 1.7 mm). Bathymetric depth was not assessed as neither sculpin species were collected in depths <30 m.

Stable isotopes and isotopic niche area and overlap

Values of $\delta^{13}\text{C}$ ranged from -21.8 ± 0.1 (mean \pm SE) in round goby to -24.7 ± 0.1 in deepwater sculpin, and $\delta^{15}\text{N}$ ranged from 12.6 \pm 0.04 in alewife to 16.9 \pm 0.04 in deepwater sculpin (Table 2).

Across all seasons, quadrats, and bathymetric depths, round goby had the largest isotopic niche area (6.1‰², SEA_C), followed by alewife (3.4‰²), while rainbow smelt, slimy sculpin, and deepwater sculpin had the smallest (1.7–1.8‰²; Table 3; Fig. 2). This relative ranking of prey fish species by SEA_C remained even when data were analyzed by season, bathymetric depth, or quadrat (Table 3). With the exception of alewife, there was a general trend towards smaller SEA_C as season progressed from spring to fall, with no obvious trends with quadrat or bathymetric depth.

Only the slimy and deepwater sculpins showed large isotopic niche overlap (63% to 69% between sculpin species; Table 3; Fig. 2). Round goby isotopic niche overlapped 15% with rainbow smelt, which accounted for 4% of round goby's isotopic niche width. No other species showed any isotopic niche overlap (Table 3; Fig. 2).

GLM regressions

For alewife, minimal adequate models indicated that quadrat, season, and total length and most of the corresponding interactions were significant, but bathymetric depth was not an important predictor for either isotope; more variation was explained in alewife $\delta^{15}\text{N}$ (60.9%) than $\delta^{13}\text{C}$ (18.5%) (Table 4). The direction and strength of the total body length – $\delta^{15}\text{N}$ relationship in alewife varied by season and quadrat (Fig. 3); $\delta^{15}\text{N}$ decreased with size in the spring season for all quadrats (all quadrats during spring: $p < 0.001$; northwest $R^2 = 0.446$, northeast $R^2 = 0.285$, southwest $R^2 = 0.292$, southeast $R^2 = 0.323$) but increased during the summer months (all quadrats during summer: $p < 0.001$; northwest $R^2 = 0.191$, southwest $R^2 = 0.275$, southeast $R^2 = 0.629$) except in the northeast quadrat ($p = 0.305$, $R^2 = 0.009$); only in the southeast quadrat was the total body length – $\delta^{15}\text{N}$ relationship significant during the fall season ($p < 0.001$, $R^2 = 0.419$). Fewer total body length – $\delta^{13}\text{C}$ relationships were significant for alewife, as $\delta^{13}\text{C}$ increased with size across all quadrats during the spring season except in the northwest quadrat (data not shown). Variation in $\delta^{13}\text{C}$ was related to size and quadrat in the summer season, but size was important only in the northwest quadrat during the fall season (data not shown).

Rainbow smelt stable isotopes GLMs explained 54.8% and 31.9% of the variability in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, respectively, with all four

Fig. 2. Stable isotope biplot for alewife, rainbow smelt, round goby, deepwater sculpin, and slimy sculpin collected from Lake Ontario in 2013. Thick circles enclose standard (40%) ellipse areas (SEA_{40}) for all species, with alewife represented by a long dashed grey circle, rainbow smelt by a solid black circle, round goby by a short dashed black circle, deepwater sculpin by a long dashed black circle, and slimy sculpin by a solid grey circle. Individual data points (light grey) are represented by crosses for alewife, diamonds for rainbow smelt, triangles for round goby, circles for deepwater sculpin, and \times symbols for slimy sculpin.

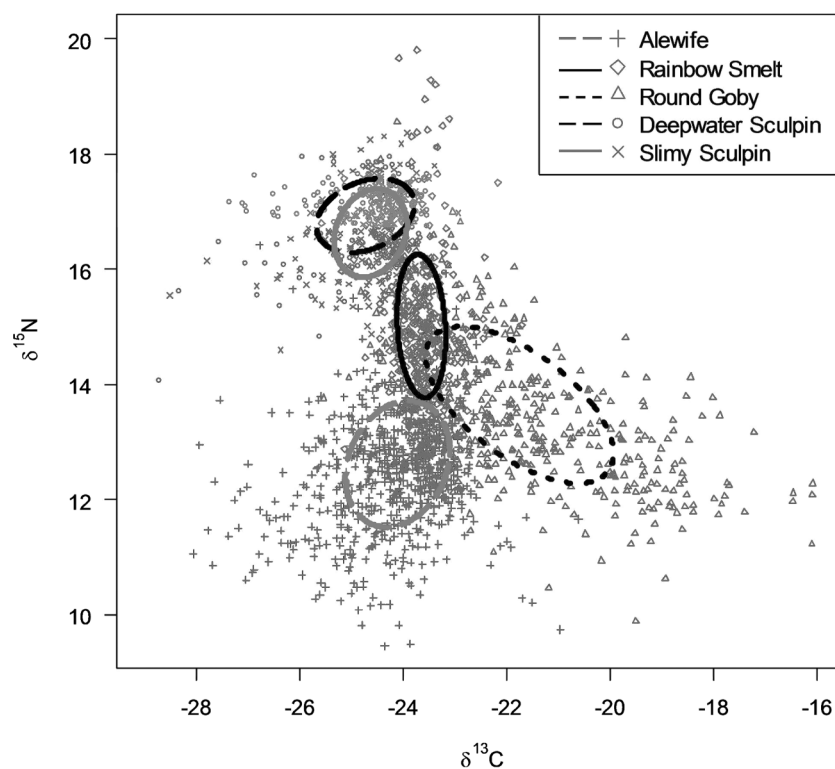
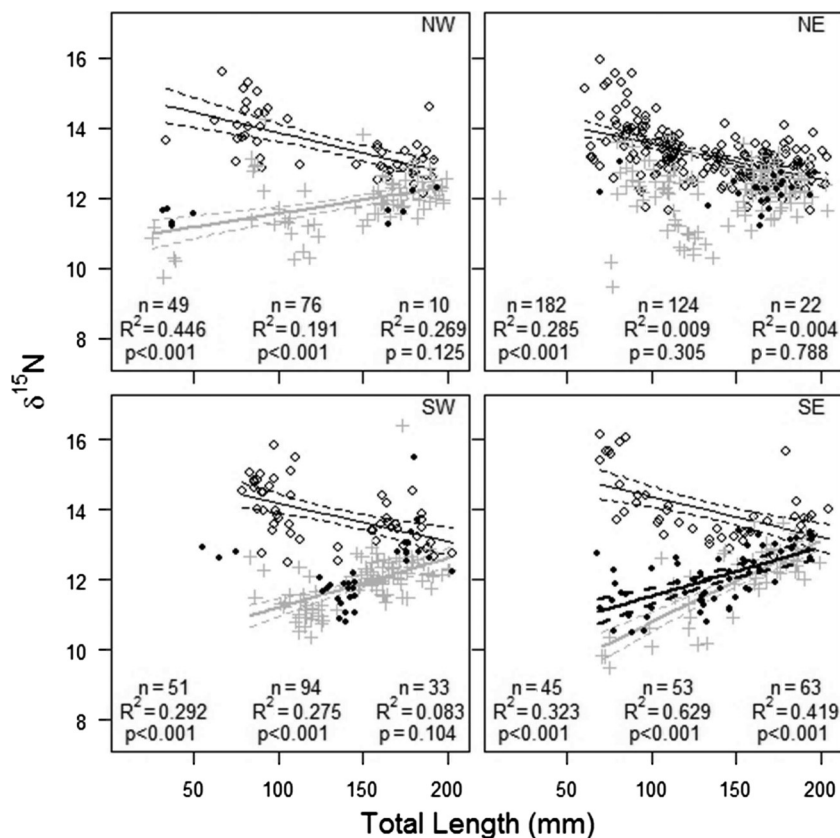


Table 4. Details and formulation of the minimal adequate models for each species–isotope combination.

Species	Isotope	Minimal adequate model	Error	Link	Residual deviance	Residual df	Null deviance	Null df	Deviance explained
Alewife	$\delta^{13}\text{C}$	$\sim \text{QUAD} + \text{SEAS} + \text{TL} + \text{QUAD} \times \text{SEAS} + \text{QUAD} \times \text{TL} + \text{SEAS} \times \text{TL} + \text{QUAD} \times \text{SEAS} \times \text{TL}$	Gaussian	Identity	662.4	776	812.3	799	18.5%
	$\delta^{15}\text{N}$	$\sim \text{QUAD} + \text{SEAS} + \text{TL} + \text{QUAD} \times \text{SEAS} + \text{QUAD} \times \text{TL} + \text{SEAS} \times \text{TL} + \text{QUAD} \times \text{SEAS} \times \text{TL}$	Gaussian	Identity	375.7	776	961.0	799	60.9%
Rainbow smelt	$\delta^{13}\text{C}$	$\sim \text{QUAD} + \text{SEA} + \text{D30} + \text{TL} + \text{QUAD} \times \text{SEA} + \text{QUAD} \times \text{D30} + \text{QUAD} \times \text{TL} + \text{SEA} \times \text{D30} + \text{SEA} \times \text{TL} + \text{D30} \times \text{TL} + \text{QUAD} \times \text{SEA} \times \text{D30} + \text{SEA} \times \text{D30} \times \text{TL}$	Gaussian	Identity	52.9	336	77.7	354	31.9%
	$\delta^{15}\text{N}$	$\sim \text{SEA} \times \text{D30} + \text{SEA} \times \text{TL} + \text{D30} \times \text{TL} + \text{Q:SEA} \times \text{D30} + \text{SEA} \times \text{D30} \times \text{TL}$	Gamma	Identity	1.1	339	2.3	354	54.8%
Round goby	$\delta^{13}\text{C}$	$\sim \text{QUAD} + \text{SEA} + \text{D30} + \text{TL} + \text{QUAD} \times \text{SEA} + \text{QUAD} \times \text{D30} + \text{QUAD} \times \text{TL} + \text{SEA} \times \text{D30} + \text{SEA} \times \text{TL} + \text{D30} \times \text{TL} + \text{QUAD} \times \text{SEA} \times \text{D30}$	Gaussian	Identity	847.2	431	1466.1	447	42.2%
	$\delta^{15}\text{N}$	$\sim \text{QUAD} + \text{SEA} + \text{D30} + \text{TL} + \text{QUAD} \times \text{SEA} + \text{QUAD} \times \text{D30} + \text{QUAD} \times \text{TL} + \text{SEA} \times \text{D30} + \text{SEA} \times \text{TL} + \text{D30} \times \text{TL} + \text{QUAD} \times \text{SEA} \times \text{D30}$	Gamma	Identity	1.6	429	4.3	447	63.0%
Deepwater sculpin	$\delta^{13}\text{C}$	$\sim \text{SEAS}$	Gamma	Identity	0.3	217	0.3	219	4.5%
	$\delta^{15}\text{N}$	$\sim \text{QUAD} + \text{SEA} + \text{TL} + \text{QUAD} \times \text{SEA} + \text{SEA} \times \text{TL}$	Gamma	Identity	0.2	215	0.3	222	51.8%
Slimy sculpin	$\delta^{13}\text{C}$	$\sim \text{QUAD} + \text{SEA} + \text{TL} + \text{QUAD} \times \text{SEA}$	Gamma	Identity	0.2	202	0.2	208	6.8%
	$\delta^{15}\text{N}$	$\sim \text{SEAS}$	Gaussian	Identity	106.8	205	119.1	205	57.4%

Note: Minimal adequate models with <50% deviance explained were not included as figures. QUAD = quadrat, SEAS = season, D30 = nearshore–offshore break point, and TL = total length (mm).

Fig. 3. The relationship between total length (mm) of alewife and $\delta^{15}\text{N}$ values for each quadrat (NW = northwest, NE = northeast, SW = southwest, and SE = southeast) and season (spring = black open diamonds, summer = grey crosses, and fall = black solid dots) collected in Lake Ontario in 2013. Sample size (n), R^2 values, and p values for the regressions by season (spring, summer, fall; left to right) are indicated at the bottom of each panel. Regression lines and 95% confidence intervals are shown only for significant total body length – $\delta^{15}\text{N}$ regressions.



explanatory variables and most of the corresponding interactions being significant (Table 2). The total body length – $\delta^{15}\text{N}$ relationship decreased for rainbow smelt during the spring season ($p < 0.001$, $R^2 = 0.354$) but was not significant for the summer ($p = 0.111$, $R^2 = 0.034$) and fall seasons ($p = 0.968$, $R^2 < 0.001$; Fig. 4a). Rainbow smelt $\delta^{13}\text{C}$ increased with increasing total length only in the northwest and northeast quadrats during the spring season, with no significant $\delta^{13}\text{C}$ trends observed in the southwest and southeast quadrats (data not shown). Carbon ($\delta^{13}\text{C}$) increased with increasing total length in the northeast quadrats during the summer season; however, no other significant trends were detected in the other quadrats during the summer season (data not shown). No significant trends were observed in the fall season in any of the quadrats (data not shown).

For round goby, minimal adequate models explained 63.0% and 42.2% of the variability in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, respectively, with all four variables and most of the corresponding interactions significant (Table 4). Round goby $\delta^{13}\text{C}$ decreased with increasing total length only in the summer season except in the southwest quadrat (no significant $\delta^{13}\text{C}$ trend observed) and only in the southeast quadrat during the fall season (data not shown). No significant $\delta^{13}\text{C}$ trends were observed in the other season–quadrat combinations (data not shown). A positive total body length – $\delta^{15}\text{N}$ relationship was significant for round goby in spring ($p = 0.003$, $R^2 = 0.003$) and summer seasons ($p = 0.030$, $R^2 = 0.043$) but not in the fall season ($p = 0.598$, $R^2 = 0.001$; Fig. 4b). Values of $\delta^{15}\text{N}$ also varied between the north and south quadrats (the respective east and west quadrats were merged, since low sample number in the four quadrat system did not produce significant isotopic differences between the nearshore and offshore (i.e., bathymetric depth)) in each season (Fig. 5). Round goby $\delta^{15}\text{N}$ was higher in the offshore in

all seasons (Fig. 6). Values of $\delta^{13}\text{C}$ were also merged between the north and south quadrats but did not yield significant results.

Stable isotopes in deepwater and slimy sculpins were not influenced by most of the variables or interactions (Table 2). Models for $\delta^{13}\text{C}$ explained a very small proportion of the variability in deepwater sculpin (4.5%) and slimy sculpin (6.8%), but models explained more variability for $\delta^{15}\text{N}$ (51.8% for deepwater sculpin; 57.4% for slimy sculpin). For deepwater sculpin, $\delta^{15}\text{N}$ increased significantly with total length in all seasons (spring: $p < 0.001$, $R^2 = 0.177$; summer: $p = 0.012$, $R^2 = 0.136$; fall: $p < 0.001$, $R^2 = 0.422$; Fig. 4c). For slimy sculpin, $\delta^{15}\text{N}$ was found to significantly decrease through the year, with the lowest values observed in the fall season ($16.3\% \pm 0.1\%$, mean \pm SE) compared with $16.8\% \pm 0.1\%$ during the spring and summer seasons (Fig. 7).

Discussion

The very limited extent of isotopic niche overlap in Lake Ontario offshore forage fish suggests high resource and habitat partitioning, with the exception of the native species (deepwater and slimy sculpins) and is intriguing. Restoration of the Great Lake's native fish community is challenged by the desire to reestablish native predator and prey species while assessing and managing the potentially ecologically disruptive consequences, but is important for valuable recreational fisheries, as well as invasive or intentionally introduced non-native species. In Lake Ontario, the current species suite is primarily a mix of non-native species with virtually no evolutionary sympatry (Mills et al. 2005). The large isotopic niche of non-native alewife and round goby may help to explain their high abundance in Lake Ontario, although further

Fig. 4. The relationship between total length (mm) of (a) rainbow smelt, (b) round goby, and (c) deepwater sculpin and $\delta^{15}\text{N}$ values by season (spring, summer, and fall) collected in Lake Ontario in 2013. Sample size (n), R^2 values, and p values for the regressions are indicated at the bottom of each panel. Regression lines and 95% confidence intervals shown only for significant total body length – $\delta^{15}\text{N}$ regressions.

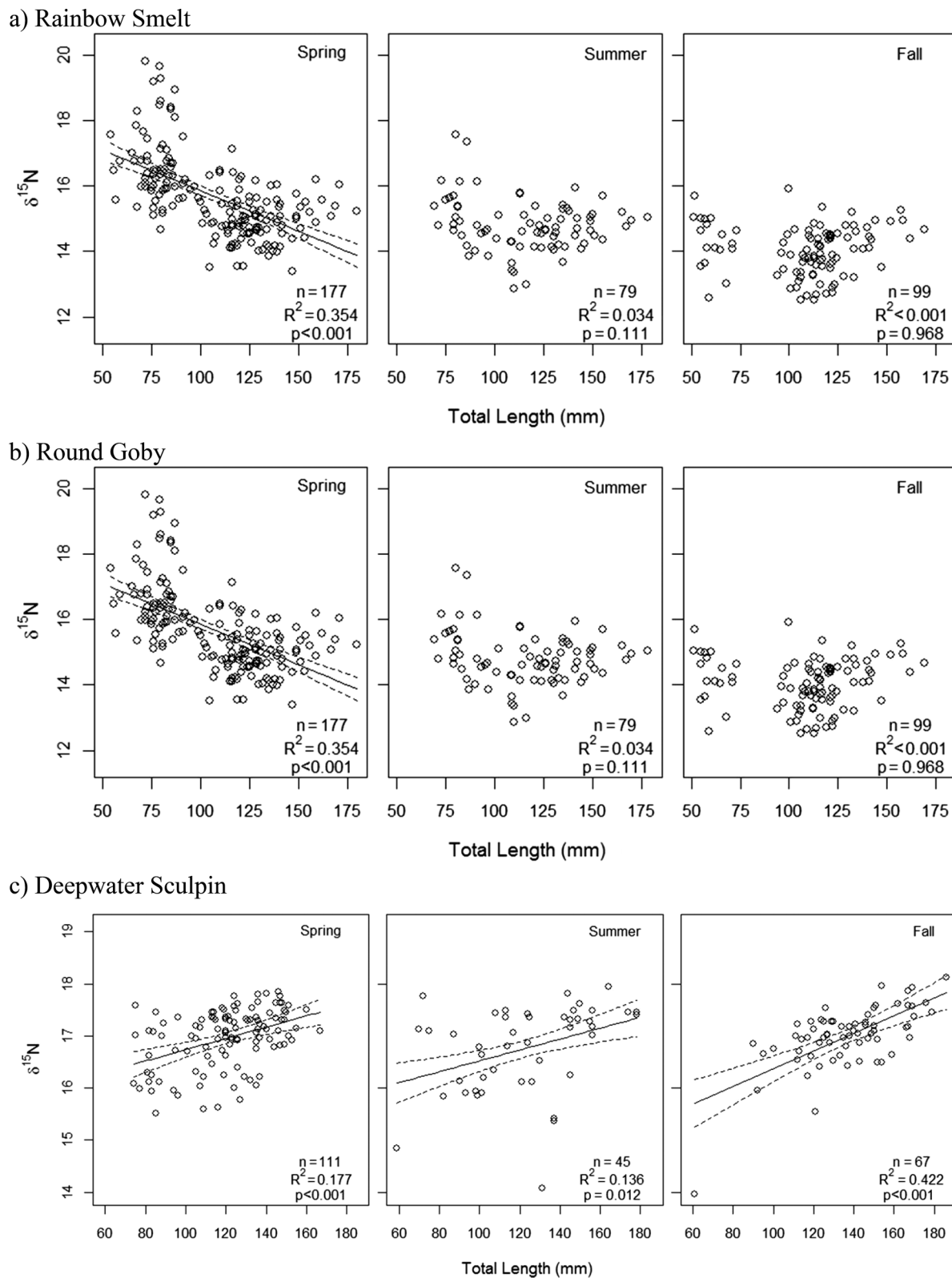


Fig. 5. Box plots of round goby $\delta^{15}\text{N}$ values between the north and south shores of Lake Ontario (north = northwest and northeast quadrats combined; south = southwest and southeast quadrats combined) and season (spring, summer, and fall). The rectangle spans the 25th and 75th percentiles, the horizontal line inside the rectangle is the median, and the whiskers indicate the minimum and maximum values. Outliers (outside the percentile range) are indicated by open circles. Sample sizes (n) for each season are indicated at the bottom of each panel.

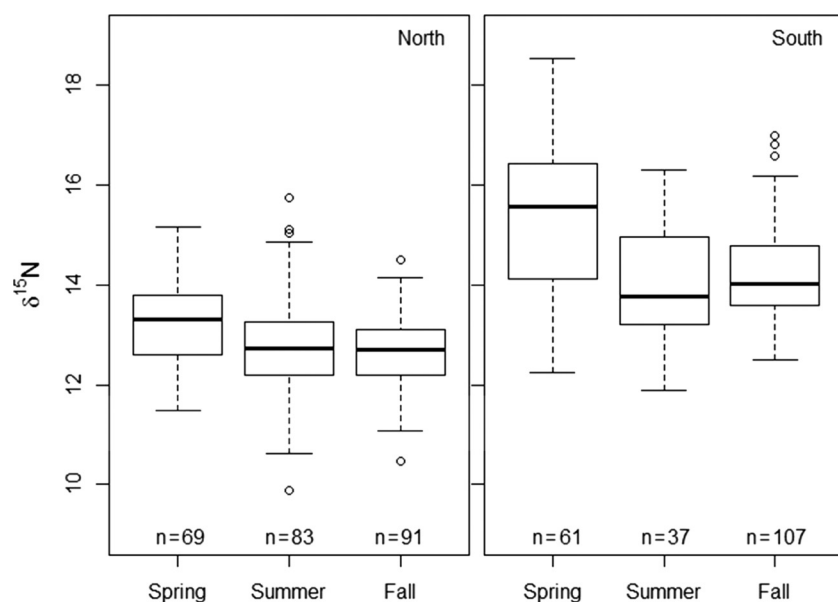
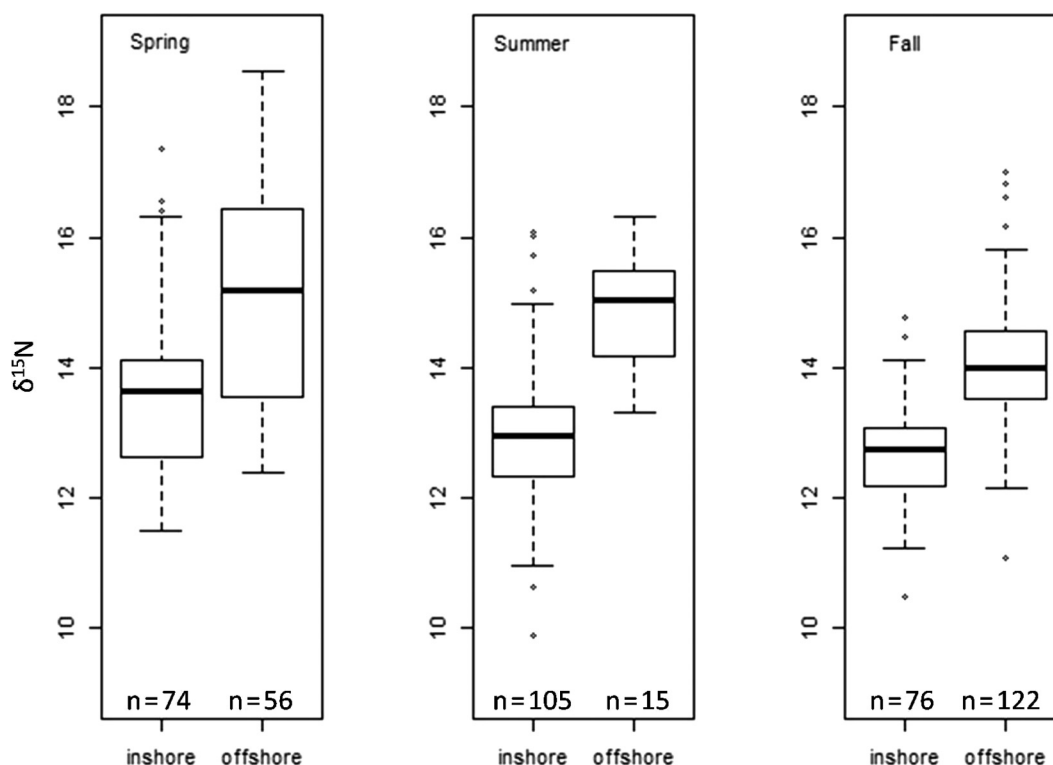


Fig. 6. Box plots of round goby $\delta^{15}\text{N}$ values between bathymetric depth (nearshore <30 m and offshore >30 m) and season (spring, summer, and fall). The rectangle spans the 25th and 75th percentiles, the horizontal line inside the rectangle is the median, and the whiskers indicate the minimum and maximum values. Outliers (outside the percentile range) are indicated by open circles. Sample sizes (n) for each season and depth category are indicated at the bottom of each panel.

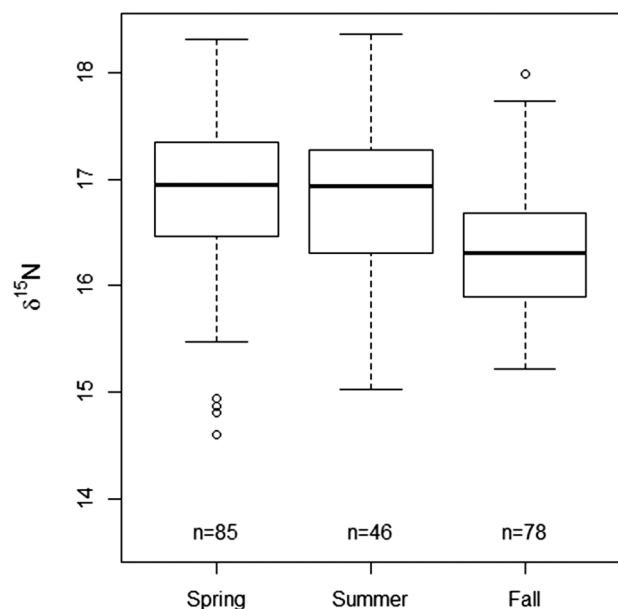


research is needed to confirm. Stable isotopes suggest unique trophic and habitat use within regions (quadrat) of Lake Ontario for non-native alewife, rainbow smelt, and round goby, which varied between seasons for some species.

Isotopic niche width and overlap

Given their high abundance, broad distribution, and increasing importance as prey to a number of top predators (Rush et al. 2012; Hebert et al. 2014), round goby are an important, unique, and

Fig. 7. Box plots of slimy sculpin $\delta^{15}\text{N}$ values for each season (spring, summer, and fall). The rectangle spans the 25th and 75th percentiles, the horizontal line inside the rectangle is the median, and the whiskers indicate the minimum and maximum values. Outliers (outside the percentile range) are indicated by open circles. Sample sizes (n) for each season are indicated at the bottom.



integrative trophic link in the Lake Ontario food web. Round goby had the largest overall isotopic niche width (6.1‰), almost twice as large as alewife and over three times the area of the other prey fish species. The larger niche width is mostly influenced by variation in $\delta^{13}\text{C}$ values. Round goby inhabit both deep water and littoral zones and appear to migrate between these habitats seasonally (Bunnell et al. 2005; Walsh et al. 2007). Round goby have been observed in multiple habitats and have moderately high site affinity once a home range has been established (Charlebois et al. 1997; Ray and Corkum 2001). Variation in isotopic signatures may reflect regional and even smaller-scale differences in carbon sources and habitat use. Additional variation in isotope values may also be associated with ontogenetic changes in the diet of round goby (Barton et al. 2005; Brush et al. 2012), corroborated by our evidence of a significant TL–isotope relationship. Stomach content analysis indicated that round goby diets are dominated by dreissenid mussel, and isotopic signatures do not suggest otherwise (but see Brush et al. 2012). As a species, round goby are integrating a wide range of carbon sources from different habitats.

The unique isotopic niche of the alewife compared with the other prey fish in the lower region $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ biplot is consistent with their offshore pelagic habitat use (Wells 1968) and diet dominated by zooplankton, including primary consumers (Stewart et al. 2009; Stewart and Sprules 2011; Bunnell et al. 2015). Seasonal and spatial variation in isotopic niche in alewife likely reflects seasonal and spatial variation in stable isotope values in plankton, as has been observed in other Great Lakes (Driscoll et al. 2015). It could also be influenced by shifts in diet due to variation in zooplankton abundance and diversity over season and space in Lake Ontario (Stewart et al. 2009). Some variation in alewife isotopes may also reflect predation on fish fry at certain times of the year, although this is thought to be infrequent in Lake Ontario (Krueger et al. 1995). O’Gorman et al. (2000) found alewife spring distribution shifted to deeper waters immediately following the invasion of dreissenids in the early 1990s. However, Rush et al. (2012) presented stable isotope data on alewife at discrete times from 1995 to 2008, and those data, in combination with our own, show high

variation but no trend through time in either $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$, suggesting little change in alewife trophic position in the past 20 years. There is evidence that alewife in Lake Ontario increased their trophic position from the early 1970s to the mid-1990s, due to high amounts of *Mysis* and predatory cladocerans in their diets in the 1990s and early 2000s (Stewart et al. 2009). The year-to-year variability in alewife $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ likely reflects variation in prey type and potentially to seasonal variability in the isotope values of zooplankton (Turschak and Bootsma 2015).

Stable isotopes suggest that rainbow smelt also have a unique niche compared with other prey fish species. The large variation in their $\delta^{15}\text{N}$ values is consistent with stomach content analysis that suggests that Lake Ontario and other Great Lakes rainbow smelt feed at many trophic positions and shift to feeding at higher trophic positions as they grow (Brandt and Madon 1986; Lantry 1991; Lantry and Stewart 1993; Stewart 2010; Stewart and Sprules 2011). The relatively narrow range of $\delta^{13}\text{C}$ values compared with other prey fish species suggests that rainbow smelt may occupy a relatively narrow range of offshore habitat.

A high reliance on *Mysis* for food (Lantry 1991; Lantry and Stewart 1993; Stewart and Sprules 2011) may be a dominant influence on the rainbow smelt isotopic niche. The most recent stomach content analysis of Lake Ontario adult rainbow smelt indicated that 98% of the diet by mass was *Mysis* (Stewart 2010; Stewart and Sprules 2011). *Mysis* are omnivores and feed across a diverse range of trophic positions (Parker 1980; Pennak 1978; Johannsson et al. 2001; Johannsson 2003; Bailey et al. 2006).

Like rainbow smelt, sculpin diets are also most likely highly dominated by *Mysis* (Walsh et al. 2008; Stewart and Sprules 2011), yet the sculpin species and rainbow smelt had very different isotopic niches. *Mysis* isotopic values vary with depth (Sierszen et al. 2011), and in deeper regions $\delta^{15}\text{N}$ may be higher at a given trophic level due to benthic nutrient cycling in the offshore (Sierszen et al. 2011). It may be that the benthic sculpins are feeding on deeper and more bottom-oriented *Mysis* individuals than the pelagic rainbow smelt. Variation in isotopic niche of their common, but habitat-specific, *Mysis* prey may account for the niche separation, not a difference in their trophic position. There is also evidence that sculpin species can feed on eggs from a wide variety of fish species in Lake Michigan, although the lake-wide mean was $\sim 10\%$ of the dry mass of the stomach contents (Mychek-Londer et al. 2013); evidence for this in Lake Ontario is lacking.

Isotopic niche overlap between rainbow smelt and round goby was $<15\%$, suggesting that these species may share some resources. Given the benthic life history of the round goby, this overlap is likely benthic invertebrates, such as from the Order Diptera (e.g., Chironomidae), which has been reported as a diet item for both species, although more water column situated species (e.g., Copepoda, *Mysis*) have also been reported for both (Evans and Loftus 1987; Stewart and Sprules 2011; Brush et al. 2012; Mychek-Londer et al. 2013). Whether this 15% overlap is significant to either population is difficult to assess with these data.

The two sculpin species, deepwater and slimy, had the highest $\delta^{15}\text{N}$ values and no isotopic niche overlap with the other species. Historically, *Diporeia* spp. and *Mysis* were the major prey items of both deepwater and slimy sculpins (Kraft 1977; Wells 1980), and studies in Lake Michigan have shown very similar stable isotope values between these benthic invertebrates (Turschak and Bootsma 2015). *Diporeia* abundance decreased in the 1990s in Lake Ontario (Dermott 2001; Lozano et al. 2001; Birkett et al. 2015), and more recent diet of Lake Ontario slimy sculpin diet consists mainly of *Mysis*, although slimy sculpin continue to favour *Diporeia* spp. when available (Walsh et al. 2008; Stewart and Sprules 2011). The sculpin species reside in the deep zones (>30 m) of Lake Ontario, with little to no migration to the nearshore and are clearly utilizing a unique source of deepwater carbon. As discussed above, the elevated $\delta^{15}\text{N}$ values may be caused by benthic nutrient cycling in the offshore (Mulholland et al. 2000) rather than feeding at a

higher trophic level than the other prey fish species. Assessment of variation in Lake Ontario *Mysis* isotopic values as a function of depth would be informative in this regard.

The highest isotopic niche overlap was found between the sculpin species (>63%), and this result suggests an increased potential for competition between these species, especially with the recent increase in the density of deepwater sculpin individuals (Weidel and Walsh 2015). Diet overlap indexes based on stomach contents in the Great Lakes basin indicated that these sculpin species had high diet overlap (51%, Hondorp et al. 2005; and >60%, Martin 1984). The higher overlap observed in our study may reflect a decrease in *Diporeia* and greater reliance on *Mysis*; in other Great Lakes, *Mysis* contribute to the majority of the deepwater sculpin diet (Mychek-Londer et al. 2013). The differences between the sculpin species likely reflects a more varied diet in the slimy sculpin. From studies in Lake Michigan, slimy sculpin consumed proportionally more *Limnocalanus macrurus* than *Mysis* (0.48 versus 0.19), whereas the deepwater sculpin focused on *Mysis* (0.61) (Mychek-Londer et al. 2013).

Factors influencing variation in stable isotopes

Variation in the rainbow smelt and alewife isotope values across quadrats suggest that these species can use food and habitat resources differently depending on local conditions. It is important to stress that variation in baseline isotopes could also be a factor in these trends (i.e., diet are similar but isotope values in prey vary with space), although evidence from other studies suggest that food resources can vary spatially. Variation in abiotic conditions (temperature, upwelling frequency, land use, proximity to major tributaries) among regions (Minns and Wichert 2005; Howell et al. 2012a, 2012b) can lead to heterogeneity in food resources, including seasonal variation in development time, distribution, and species composition of invertebrate food resources (Patalas 1969; Johannsson 1995; Johannsson and O'Gorman 1991; Benoît et al. 2002). This can result in high regional variation in prey fish species diet (Stewart et al. 2009) and presumably habitat use. It is unknown whether the apparent regional variation in diet and habitat use, suggested by these results, is persistent from year to year.

In addition to quadrat, variation in alewife $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were influenced by body length and season. For the larger alewife (>150 mm), isotope values were consistent across season. In the spring season, the $\delta^{15}\text{N}$ of smaller alewife was elevated. This suggests that the smaller subadult alewife may be feeding at a high trophic position in early spring or over winter than larger alewife. We know of no independent data that supports this contention. In early spring, stomach content analysis suggests adult and subadult alewife diets are very similar (Stewart et al. 2009). Seasonal variation in $\delta^{15}\text{N}$ observed in zooplankton in the Great Lakes (Driscoll et al. 2015) could explain the higher values in small alewife, as these smaller fish would reflect changes in prey isotope values more quickly than larger individuals. As well, overwinter yearling alewife are more nearshore than adults (Bergstedt and O'Gorman 1989), and this difference in distribution probably extends throughout the spring season. Alewife are known to feed on the larvae of other fish species (Krueger et al. 1995; Madenjian et al. 2008), and it may be that subadult alewife are feeding on larval or juvenile fish or fish eggs in the nearshore during the winter and early spring.

Carbon stable isotope values showed similar trends to $\delta^{15}\text{N}$ in alewife, but explained a third of the variation. During the spring season, $\delta^{13}\text{C}$ decreased with increasing size during the spring, suggesting larger alewife are further offshore than smaller individuals. O'Gorman et al. (2000) found that over a 20-year period, adult alewife were more abundant in deeper locations than yearlings during the spring. Alternatively, larger alewife could be feeding on different prey, although stomach content analysis has not found differences across size classes (Stewart et al. 2009).

Stewart et al. (2009) observed that adult Lake Ontario alewife fed mostly on *Mysis* at bathymetric depths greater than 70 m where *Mysis* are abundant and mostly on zooplankton in shallower waters. Lake Ontario *Mysis* were determined to have a higher trophic position (2.5–2.6) than zooplankton (2.1–2.4; Stewart and Sprules 2011). Offshore alewife feeding mostly on *Mysis* should have higher $\delta^{15}\text{N}$ values, but this was not observed, perhaps because a majority of the alewife samples were caught in gillnets and diets may no longer vary with bathymetric depth. It is also possible that sampling and observational variation in isotopic values precludes detecting small differences in trophic position, as 30 m bathymetric depth was used to distinguish nearshore and offshore. Alternatively, seasonal changes in distribution and diet of alewife might mean that isotopic signatures, reflecting the diet and habitat use of alewife over months, might obscure finer temporal or spatial variation in diet and habitat use. As well, seasonal changes in isotope values in prey could be contributing to this trend. Alewife, rainbow smelt, and round goby isotopic signatures all varied with quadrat, suggesting differences in trophic ecology of these species across space, at least a large regional scale. The ecological importance of this spatial variation and its potential effect on inferring diets from isotopic mixing models of predators requires more investigation.

Rainbow smelt $\delta^{15}\text{N}$ decreased with increasing total length during the spring season, which is similar to alewife and might be driven by more rapid changes in isotopes in the smaller smelt. During nonstratified periods, rainbow smelt feed throughout the water column (Nellbring 1989), perhaps causing small individuals to consume benthic species including mysids and other invertebrates potentially high in $\delta^{15}\text{N}$. This time of year would also allow larger piscivorous adults to consume other pelagic fishes (i.e., juvenile alewife), which may not be available during high stratification periods (e.g., summer), as well as on young-of-the-year rainbow smelt (Lantry and Stewart 2000) or slimy sculpin (Brandt and Madon 1986). Thermal stratification may isolate rainbow smelt within the hypolimnion. Evans and Loftus (1987) suggested that during high water stratification, both young and adult rainbow smelt consume similar prey resources, but separate themselves within the water column due to differences in diel behaviours. This spatial structure would allow both young and adults to feed on mysids, which would account for comparable $\delta^{15}\text{N}$ values. This foraging behaviour appears to be present during the early fall as the thermocline has not yet fully disintegrated (Brandt and Madon 1986). In the northeast quadrat, $\delta^{13}\text{C}$ increased with total length in both the spring and summer seasons, suggesting adults are associated more with the benthos in this region.

Variance partitioning models were strongest for $\delta^{13}\text{C}$ in round goby than for any of the other prey fish species in Lake Ontario, which makes sense given the benthic habitat use, limited summer home range, and proposed seasonal migration to deeper waters in the winter. Variance partitioning models for $\delta^{15}\text{N}$ were also strongest for round goby than for any other prey fish species and was probably related to round goby migration and a change in $\delta^{15}\text{N}$ over size. Larger individuals appear to be specialists, perhaps feeding exclusively on dreissenid mussels, although there is evidence that round goby may prefer other prey over these mussels (Brush et al. 2012). Smaller round gobies have been found to consume a more varied diet while inhabiting the nearshore and tributaries (Barton et al. 2005; Pennuto et al. 2010) and perhaps could be generalists. In the Kingston Basin, diet differences were observed between small and large individuals during the spring (Brush et al. 2012). Diets appear to become similar in the summer season as larger individuals migrate into the nearshore. The large isotopic range of round gobies collected in the fall season, especially small individuals, suggest a diverse diet, again perhaps due to the beginning of migration to deeper locations.

There was minimal change to the isotopic niche area in both sculpin species by quadrat and season, and stable isotope values

were not influenced by quadrat and season, which suggests small differences in the diet and likely very little spatial variation in the stable isotopes of the deepwater zone of Lake Ontario. Differences in isotopic niche between these species may reflect slimy sculpin focusing more on non-*Mysis* prey, such as chironomids, which have been observed in Lake Michigan (Bunnell et al. 2015). Models explained very little of the $\delta^{13}\text{C}$ variation in both sculpin species, which would suggest that species are occupying a more homogeneous deepwater habitat with common sources of carbon. However, as these species co-inhabit the deepwater region of Lake Ontario (>30 m), stable isotopes may not be able to detect regional differences, if any, due to a limited prey base and prey preference and as well as the homogenization of the offshore lake benthic environment.

Ontogenetic shifts in diet are present in deepwater sculpin (59 to 186 mm total length) based on $\delta^{15}\text{N}$ -length relationships; no other variables were important in this species. Similar shifts were observed for Lake Michigan deepwater sculpin (Turschak and Bootsma 2015). Slimy sculpin displayed a significant reduction in $\delta^{15}\text{N}$ with season, with lower values in the fall, but no other variables influenced $\delta^{15}\text{N}$ in this species. With limited deepwater information on seasonal changes in invertebrates, it is hard to explain the seasonal changes seen in the slimy sculpin; no seasonal trends were observed in the diet of this species in Lake Michigan (Bunnell et al. 2015). Prior to the decline of *Diporeia*, Kraft and Kitchell (1986) found that larger deepwater sculpin did not consume larger prey items, but now with the near absence of *Diporeia* in the Great Lakes, the size of deepwater sculpin may be positively correlated with the size of their *Mysis* prey. *Leptodiaptomus sicilis* and *Limnocalanus macrurus* are common large-bodied calanoids found below the thermocline in Lake Ontario (Rudstam et al. 2015), which could be common in the deepwater sculpin diet. Smaller deepwater sculpin (50–90 mm; from Brandt 1986) may be consuming a higher proportion of these calanoid species relative to larger deepwater sculpin to compensate for the loss of *Diporeia*, as this size cohort may not have the gape size to ingest larger *Mysis*. The consumption of *L. sicilis* and *L. macrurus* would decrease the $\delta^{15}\text{N}$ in smaller individuals, although $\delta^{15}\text{N}$ in *L. macrurus* was similar to that of *Mysis* in Lake Ontario (Driscoll et al. 2015). There was also a larger variation in $\delta^{15}\text{N}$ values in smaller deepwater sculpin, which suggested that this size group is consuming a larger diversity of prey, perhaps associated with shifts in diet as they grow.

Although we reached our aims in this study, there were limitations to the sampling and GLM analysis. In some cases, when testing variables and interactions there was evidence of non-normal distribution of the isotope data with strong tails (i.e., high skewness). This error likely arose because of the overall lower sample sizes when separating the isotopic data or the potential presence of bimodal distributions. Variables and interactions resulting with low sample sizes also probably contributed to spurious correlations within the GLM analysis. For precaution, only the strongest relationships (>50% deviance explained) were discussed and considered to be viable as some of the models may be over-parameterized even when using this large isotopic data set.

Summary

This study confirms that concurrent stable isotopes analysis of coexisting, and potentially competing, prey fish species provides information of both ecological and management interest. Limited spatial variation in isotopic niche-space metrics for species among quadrats suggests that coexisting prey fish community trophic ecology and habitat use is structured in a similar way across the entire lake. This regional persistence suggests that the observed structure may be adaptive, serve to reduce competition, and will likely be expressed similarly in other systems inhabited by these species combinations. However, species-specific isotopic values varied with quadrat for all species and with depth for most (ex-

ception being alewife), suggesting regional environmental variability can modify species-specific diet and habitat use. Isotopic values also varied with size among the prey fish species (the only exception being slimy sculpin $\delta^{15}\text{N}$), but not in all seasons or quadrats, suggesting that ontogenetic-driven variation in trophic ecology may be an important structural characteristic of offshore prey fish food webs. These results support the idea that coexisting native and non-native species can evolve and potentially develop sustainable and functionally efficient food webs. From a management perspective, it may be worthwhile to consider a more conciliatory approach when managing a well-established non-native species assemblage by recognizing the value of novel species (Carroll 2011) rather than always framing the native–non-native species management and ecosystem restoration discussion as a dilemma (Stewart et al. 1999; Dettmers et al. 2012; Claramunt and Clapp 2014).

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